at a distant location (e.g., with growth of synapse diameter), quantal size would not be increased.

Reconciling Evidence for Presynaptic and Postsynaptic Involvement in LTP

We now return to the question of whether the lack of change in potency observed by Enoki et al. (2009) (Figure 1) indeed rules out a significant postsynaptic contribution to LTP. Let us start by supposing that the EPSPs generated by single CA1 synapses are uniquantal. The answer is then simple: LTP could enlarge the synapse by addition of new release sites presynaptically and the addition of AMPA channels to the periphery of an enlarged postsynaptic specialization (resulting in no change in AMPAR density). By the logic of Advance 4—that quantal size is determined by local density of AMPA channels—this would not change potency. If, on the other hand, release can be multiquantal, enhancing p_r would lead to more multiquantal responses; if summation is linear, this should lead to an increase in potency, contrary to what is observed. However, if summation is sublinear, as suggested by Advance 3, large responses would be choked off, leading to little change in potency. In summary, the fact that LTP does not affect potency is not a definitive argument against strong postsynaptic involvement in LTP.

The newly available data from the papers reviewed here provide strong constraints on models of LTP expression. Readers interested in a model that deals with many of these complexities and accounts for a broad range of findings regarding both presynaptic and postsynaptic changes should consult Lisman and Raghavachari (2006). More constraints will be available soon as even better methods are applied to the problem. Specifically, methods that break the diffraction limit of light microscopy may make it possible to directly visualize where AMPARs are added to synapses and how synapses grow after LTP induction. The use of quantum dots will make it possible to monitor single-release events before and after LTP (Zhang et al., 2009). Buy your tickets now for the pre/post debate, 2010.

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A Nonvisual Look at the Functional Organization of Visual Cortex

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In this issue of *Neuron*, Mahon et al. show that the ventral visual cortex of congenitally blind individuals, who have never experienced the visual world, has an object-category organization similar to that found in sighted individuals. Here, we discuss the implications of this finding for our understanding of the "visual" cortex.

> "… if you take men born blind, who have made use of such [tactile] sensations all their life, you will find they feel things with perfect exactness that one might almost say that they see with their hands.…"
>
> —Descartes (1637; in Gregory and Wallace, 1963)

Visual neuroscience research has predominantly considered the visual cortex as a stimulus-driven, unimodal system. This line of research has revealed

a hierarchical organization of visual cortex. The first stage of cortical processing consists of neurons tuned to low-level visual features such as oriented bars. These neurons feed into subsequent regions sensitive to increasingly complex combinations of features such as simple shapes, which then project to higher-level visual cortex where neurons responding selectively to whole objects have been found. In humans, there is evidence for distinct regions responding selectively to images of faces, body parts, and spatial layouts (Downing et al., 2006). At a coarser anatomical level, there is a consistent animate-inanimate organization with animate objects (e.g., animals, faces) being represented more laterally than inanimate objects (e.g., tools, houses) (Chao et al., 1999). The ontogeny of the functional organization of visual cortex is under debate, with some researchers highlighting the influence of genetics, while others have focused on the role of visual experience. However, common to most accounts is that visual experience during certain critical periods is necessary for normal functional organization to develop.

In a study published in this issue of *Neuron*, Mahon et al. (2009) provide convincing evidence for a different view, by showing a regular animate-inanimate organization in the visual cortex of individuals that have had no visual experience. This finding challenges the deep-rooted notion of the visual cortex as a unimodal system, molded by visual experience.

Using fMRI, Mahon and colleagues (2009) tested a group of sighted participants on two tasks, one involving the viewing of animate and inanimate objects and the second involving a task where the participants listened to the names of these objects while judging the relative size of each of them. The same auditory task was presented to three participants who were blind from birth (congenital blindness) and thus do not have a representation of the visual world. In the sighted group, the authors found a relatively stronger response during the viewing of animate objects in lateral visual regions and during the viewing of inanimate objects in medial regions, thereby replicating the previously established animate-inanimate organization of visual cortex (Chao et al., 1999). Interestingly, this organization was also evident when the sighted group performed the auditory task, suggesting that the spoken words evoked visual representations of these objects, possibly through visual imagery. The truly remarkable finding was that the same animate-inanimate organization was also found in the visual cortex of congenitally blind participants performing the auditory task. Contrary to the results of the sighted group, this finding cannot be simply explained by referring to visual imagery or to associations of the object names with the visual appearance of the objects. Instead, the result suggests the activation of nonvisual object representations and shows that the large-scale categorical organization of ventral visual cortex is independent of visual input and visual experience.

These results raise new questions about the origins of neural response properties in the visual system, as well as in other sensory systems. What is represented or computed in higher-level visual cortex if, as Mahon and colleagues (2009) show, visual input is not critical for the functional organization of this region? Taking this one step further: how "visual" is visual cortex?

It is likely that the specific content of the representations in the visual cortex of congenitally blind individuals is quite different from that in sighted individuals. Nonetheless, the similarity in the categorical organization of higher-order visual cortex in both groups indicates that this organization does not critically depend on visual experience and may be due to more abstract relationships between object categories. Although congenitally blind individuals have had no visual experience, they have had extensive experience with the world through tactile and auditory signals and have developed increased sensitivity to these nonvisual signals. This raises the interesting possibility that high-level, and perhaps also lower-level, visual cortex can represent object features and spatial scene characteristics independently of the modality that conveys this information. In this view, visual cortex is mostly visual because this is the dominant modality for spatial information, including object shape. When vision is lost and other modalities take over as the primary source of spatial information, visual cortex may become more sensitive to the latent input from these other modalities (e.g., Pascual-Leone and Hamilton, 2001). Evidence for this view comes from studies showing activation in visual cortex when blind individuals read Braille (Sadato et al., 1996). Similarly, congenitally blind participants experiencing tactile flow show activation in areas that are, in sighted participants, activated by optic flow (Ricciardi et al., 2007). These and other studies provide evidence for the view that computations in human visual cortex need not be limited to visual input. Rather, it seems that the visual system is predisposed to process certain types of information that are mostly, but not exclusively, provided by the eyes. Experiments on the famous case S.B., a middle-aged man who regained sight after being blind for basically all his life, further suggest a convergence of tactile and visual object representations (Gregory and Wallace, 1963). For example, S.B. had learned to recognize inscribed upper case letters by touch. When his sight was restored he could quickly recognize upper case letters by sight alone, whereas he had great difficulty learning to read lower case letters. He could also draw objects from memory, including animals and tools that he had never seen. These intriguing observations suggest efficient transfer of information from touch to vision and dovetail with the surprisingly similar object-category organization in the visual cortex of congenitally blind participants as compared to sighted participants, described by Mahon and colleagues (2009).

What could be the root cause of the animate-inanimate organization of ventral visual cortex? Most accounts, naturally, are based on visual properties of object categories. For example, one proposal is that the animate-inanimate organization is related to retinal eccentricity biases that extend from early visual cortex into higher-level visual cortex (Malach et al., 2002). The argument is that animate objects, such as faces, require a detailed representation in order to be discriminated and are thus represented in the foveal (lateral) part of visual cortex, where spatial resolution is highest. By contrast, inanimate objects, such as buildings or large objects require a coarser representation to allow for large-scale integration and thus activate peripheral (medial) parts. Although visual factors, such as retinal topography, likely influence the categorical organization of visual cortex, they

cannot directly account for the animate-inanimate organization in congenitally blind individuals. Instead, Mahon et al.'s findings suggest additional organizing principles of a more abstract, nonvisual nature. Accordingly, they interpret their findings as reflecting an innate categorical organization of ventral visual cortex that is part of distributed neural circuits predisposed to process information about different conceptual domains. The interpretation in terms of an innate organization at the level of conceptual domain provides a compelling explanation for their (and other) findings. However, other interpretations cannot as of yet be excluded. For example, it is also possible that the organization is due to nonconceptual differences between animate and inanimate object categories, such as differences in the strength of contextual associations (inanimate objects are generally more strongly associated with a particular context; Bar and Aminoff, 2003), and/or motion properties (animate objects generally move more than inanimate objects, and their motion is more often articulated; Beauchamp et al., 2002). Importantly, however, Mahon et al.'s results indicate that any explanation would have to be independent of input modality, which excludes accounts that are purely visual and favors accounts that are formulated at a more abstract level.

The study opens up many interesting questions for future research. A first set of questions concerns the extent to which the organization of visual cortex extends to nonvisual processing. We can discriminate the orientation of a bar by touch (orientation discrimination), hear cars driving by (motion perception and object identification), and locate objects in space based on both auditory and somatosensory information (spatial processing). Do such tasks activate specialized regions in the visual cortex of congenitally blind individuals, as they do in the visual cortex of sighted individuals when performing these tasks using visual input? A second set of questions concerns the specificity of this organization. Mahon et al. (2009) found a coarse animate-inanimate organization spanning most of higher-level visual cortex. In sighted participants, there is also evidence for a more fine-grained functional organization. For example, faces and bodies activate nearby regions within the lateral "animate" cortex (Peelen and Downing, 2007). Is a similar fine-grained organization evident in congenitally blind participants? A third set of questions concerns the functional significance of the animate-inanimate organization in congenitally blind people. Which behaviors critically rely on the animate and inanimate regions of visual cortex? One way to test this might be to briefly disrupt neural processing using transcranial magnetic stimulation (TMS; a technique that delivers brief electric currents through a coil placed on the scalp). The "animate" region is well positioned for this technique because of its lateral location close to the skull. Is object recognition, or other tasks, disproportionally impaired for animate categories when TMS is applied? Another way to test the functional significance of the animate and inanimate regions might be to relate fMRI responses to behavioral measures on a trial-by-trial basis. Finally, tests on the functional and anatomical connectivity of the regions identified by Mahon et al. (2009) would provide more information about the networks that these regions are part of, and about possible connectivity differences between blind and sighted individuals. Answers to the above questions will provide further insight in the role of visual cortex in processing nonvisual stimuli and the extent to which the functional organization of visual cortex is determined by visual experience.

In sum, the study by Mahon et al. (2009) provides evidence for an animate-inanimate organization in ventral visual cortex that transcends the visual modality. The results suggest that representations in visual cortex may be less visual than previously thought and challenge the notion that the organization of the ventral visual cortex critically depends on visual experience.

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